






Tree genotypes affect rock lichens and understory plants: examples of trophic-independent interactions

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Abstract. Genetic variation in foundation tree species can strongly influence communities of trophic-dependent organisms, such as herbivorous insects, pollinators, and mycorrhizal fungi. However, the extent and manner in which this variation results in unexpected interactions that reach trophic-independent organisms remains poorly understood, even though these interactions are essential to understanding complex ecosystems. In pinyon–juniper woodland at Sunset Crater (Arizona, USA), we studied pinyon (*Pinus edulis*) that were either resistant or susceptible to stem-boring moths (*Dioryctria albovittella*). Moth herbivory alters the architecture of susceptible trees, thereby modifying the microhabitat beneath their crowns. We tested the hypothesis that this interaction between herbivore and tree genotype extends to affect trophic-independent communities of saxicolous (i.e., growing on rocks) lichens and bryophytes and vascular plants beneath their crowns. Under 30 pairs of moth-resistant and moth-susceptible trees, we estimated percent cover of lichens, bryophytes, and vascular plants. We also quantified the cover of leaf litter and rocks as well as light availability. Four major findings emerged. (1) Compared to moth-resistant trees, which exhibited monopodial architecture, the microhabitat under the shrub-like susceptible trees was 60% darker and had 21% more litter resulting in 68% less rock exposure. (2) Susceptible trees had 56% and 87% less cover, 42% and 80% less richness, and 38% and 92% less diversity of saxicolous and plant communities, respectively, compared to resistant trees. (3) Both saxicolous and plant species accumulated at a slower rate beneath susceptible trees, suggesting an environment that might inhibit colonization and/or growth. (4) Both saxicolous and plant communities were negatively affected by the habitat provided by susceptible trees. The results suggest that herbivory of moth-susceptible trees generated litter at high enough rates to reduce rock substrate availability, thereby suppressing the saxicolous communities. However, our results did not provide a causal pathway explaining the suppression of vascular plants. Nonetheless, the cascading effects of genetic variation in pinyon appear to extend beyond trophic-dependent moths to include trophic-independent saxicolous and vascular plant communities that are affected by specific tree–herbivore interactions that modify the local environment. We suggest that such genetically based interactions are common in nature and contribute to the evolution of complex communities.

Key words: arid lichen communities; arid vascular plant communities; community genetics; ecosystem function; foundation species; genetic variability; interspecific indirect genetic effects; saxicolous lichens and bryophytes.

INTRODUCTION

Ecological communities are often structured by a single dominant “foundation species” that strongly

influences population dynamics, community interactions, and ecosystem processes. Foundation species provide locally stable habitats required by many other organisms, and they stabilize fundamental ecosystem processes such as productivity and water balance (Dayton 1972, Ellison et al. 2005). Communities can interact with foundation species by way of mutualism, parasitism, commensalism, facilitation, and competition (Whitham et al. 2012). An increasing amount of evidence indicates that heritable genetic variation within foundation species affects community and ecosystem structure, function, relative fitness, and dynamics in terrestrial and aquatic habitats (Reusch et al. 2005,

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Whitham et al. 2006, 2008, Stultz et al. 2009a, Dattolo et al. 2017, Keith et al. 2017, Des Roches et al. 2018). Genetically based traits in foundation species can impart variation in community composition of the organisms they support, thus generating ecologically and evolutionary important interactions that influence the distributions of the dependent taxa (Whitham et al. 2006, 2020) and community interaction networks (Lamit et al. 2015a, Lau et al. 2016).

Interactions among species (e.g., predator–prey, plant–pollinator, plant–herbivore) have long been known to play central roles in structuring communities and, when the interactions are genetically based, they can influence the evolution of these communities. Such interactions among species are referred to as “interspecific indirect genetic effects” (IIGEs; Shuster et al. 2006). Without such interactions, evolution between pairs of species or whole communities would be unlikely or greatly reduced (terHorst et al. 2018, Whitham et al. 2020). While it is easy to appreciate how the interactions of strongly interrelating species such as an herbivore and its host plant could be genetically based, how those interactions could subsequently cascade to affect presumably non-interactive or unlinked species and communities such as lichens, bryophytes, or vascular plants growing beneath their habitat-providing trees, would seemingly stretch the boundaries of IIGEs. Here we explore how a genetically based plant–herbivore interaction may affect the understory lichen, bryophyte, and vascular plant communities. Although such disparate interactions are rarely examined, if common, they could greatly elucidate how community genetics influences evolution.

Pinyon (*Pinus edulis* Engelm.) is a foundation tree species and a defining component of pinyon–juniper woodland, the third largest vegetation type in the United States, where it covers about 19 million ha (Gottfried et al. 1995). Pinyon–juniper woodland dominates the area around northeastern Arizona’s Sunset Crater, which has a long history of research into the biology of foundation species, including the cascading effects that the interaction between tree genotype and herbivory have on tree architecture, mycorrhizal communities, nutrient cycling, and drought tolerance (Whitham and Mopper 1985, Gehring and Whitham 1991, Classen et al. 2007, Gehring et al. 2017). Pinyons growing at Sunset Crater are subjected to extensive herbivory by the stem-boring moth (*Dioryctria albiovittella* Hulst), whose larvae cut the resin ducts to bleed stems of defensive oleoresins (a mixture of monoterpenes, resin acids, and neutral compounds) and then feed inside the shoots distal to their initial point of entry (Stevens et al. 1988, Mopper et al. 1991, Cobb et al. 1997, Ruel and Whitham 2002). Chronic moth herbivory can alter the architecture, growth rate, and reproduction of susceptible trees (Whitham and Mopper 1985). Altered tree architecture, which includes densely crowned trees with compactly flattened tops (Fig. 1), is the result of selective

destruction of terminal shoots by the moth larvae (Brown et al. 2001). However, not all pinyons are attacked by moth larvae, and those that are resistant exhibit a monopodial growth form in which a dominant and centralized stem axis produces subordinate branches along its length (Fig. 1). Moth herbivory is mainly restricted to reproductively mature trees, which, at Sunset Crater, corresponds to pinyons older than 46 yr (Ruel and Whitham 2002). A genetic basis for moth resistance or susceptibility in pinyons at Sunset Crater is well established; variants differ in heterozygosity and allelic frequencies for two allozymes associated with herbivory (Mopper et al. 1991). Moths are the causal agent of differences in tree architecture because experimental removal of moths from susceptible trees results in recovery of the monopodial growth form (Brown et al. 2001). Where resistant and susceptible trees grow intermixed, variation in crown architecture affects understory microhabitat. For example, susceptible trees produce more litter per crown volume (Schuster et al. 2005), have higher needle decomposition rate (Chapman et al. 2003), and intercept less precipitation (Classen et al. 2005), compared to resistant trees. These changes in microhabitat in turn influence the microclimate beneath the tree crowns (Classen et al. 2007).

For communities occurring beneath trees, the accumulation of leaf litter may represent a particularly important variable because of its potential to alter chemical, moisture, and light conditions as well as to overtop and smother the lichens, bryophytes, and vascular plants (Xiong and Nilsson 1999, Natalia et al. 2008, Moore and Crawley 2014). At Sunset Crater, pinyon needle litter can take between 14 and 20 yr to decompose (Chapman et al. 2006; S. Chapman and A. Classen, *personal communication*). It is likely that the denser crown architecture and lower needle retention of susceptible trees may provide darker conditions with higher rates of leaf litter accumulation compared to resistant trees.

Genetic effects on interactions across trophic levels have been well documented in multiple systems (Crutsinger 2016, Des Roches et al. 2018), and numerous taxa that depend on pinyon for food energy are affected by the resistance to moths. For example, moth attacks significantly reduce cone production in susceptible trees, resulting in abandonment by seed-dispersing birds and lower rates of mammalian seed harvest (Christensen and Whitham 1991). Up to 600 species of the soil microbial community as well as mycorrhizal fungi differ between resistant and susceptible trees, which has implications for drought tolerance, uptake and utilization of nutrients, protection from pathogens, and plant growth (Gehring and Whitham 1991, Kuske et al. 2003, Gehring et al. 2017). Although genetic variation in foundation species can influence species and communities that depend directly on the foundation species for a source of energy, the extent and manner in which this influence reaches organisms on the same trophic level remains poorly understood. A few studies on this topic have

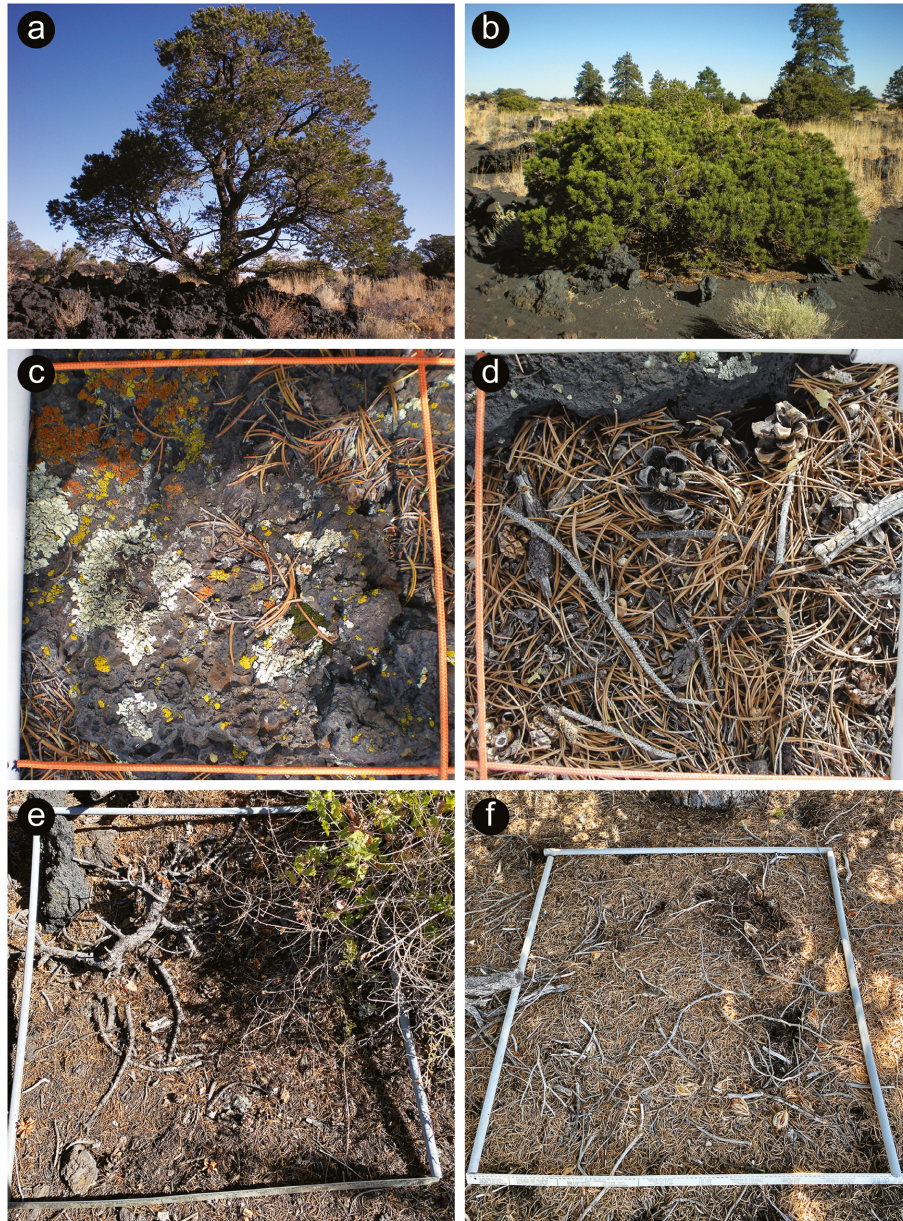


FIG. 1. Comparison of (a, b) *Pinus edulis* crown architecture, (c, d) under-crown saxicolous cover in quadrat cells, and (e, f) under-crown vascular plant cover in quadrats for trees that were resistant (a, c, e) or susceptible (b, d, f) to herbivory by larvae of the stem-boring moth (*Dioryctria albovittella*).

focused on *Populus angustifolia* James, *P. fremontii* S. Watson, and their hybrids, among which communities of understory vascular plants, epiphytic lichens, and autotrophic soil microorganisms differed (Adams et al. 2011, Lamit et al. 2011a, b, Selmants et al. 2019). The fact that genetic variation in a foundation species can influence organisms on the same trophic level has important implications for ecological processes, such as community stability and nutrient cycling (Rudgers and Maron 2003, Lankau and Strauss 2007, Keith et al. 2017).

Our overall objective is to understand the extent to which genetic variation in foundation species influences organisms, communities, and ecosystem processes at the same trophic level. Mature pinyons at Sunset Crater in Arizona present a model system for this objective because extensive and chronic herbivory by the stem-boring moth makes distinguishing resistant from susceptible trees straightforward (Whitham and Mopper 1985), and because resistance vs. susceptibility has a genetic basis and is heritable (Mopper et al. 1991, Gehring et al.

2017). Here, we examine whether the influence of this genetically based trait extends to saxicolous lichens and bryophytes and to vascular plants beneath the pinyons. We selected these groups of taxa as representatives of trophic-independent organisms that are physically detached from the foundation species, yet they occupy the habitat provided by it. We test the following primary hypothesis: community composition of lichens, bryophytes, and vascular plants is different beneath crowns of moth-resistant and susceptible pinyons, examples of IIGEs. To identify the links between pinyon genotypes that make up the two architectural phenotypes and variation in saxicolous and vascular plant communities, we also test two subordinate hypotheses: (1) increased litter accumulation beneath susceptible trees reduces lichen and bryophyte as well as vascular plant cover, richness, and diversity and (2) decreased light availability beneath moth-susceptible trees reduces lichen and bryophyte as well as vascular plant cover, richness, and diversity. This study of saxicolous and vascular plant communities beneath pinyons explores the degree to which the cascading effects of genetically based variation in a foundation species extend beyond interactions across trophic levels.

MATERIALS AND METHODS

Study site

The study was conducted adjacent to Sunset Crater National Monument, 35 km northeast of Flagstaff, Arizona, USA, 2,000 m elevation (Fig. 2). The deep cinder soils in this region are nutrient-poor, have low water-holding capacity (Cobb et al. 1997), and belong to the taxonomic subgroup Typic Ustorthent (Soil Survey Staff 1999). Rocks at the study site consist of volcanic basalt originating during the last series of eruptions at Sunset Crater, which terminated around 900 yr ago. These eruptions blanketed the landscape with approximately 8 km² of lava and 2,300 km² of tephra (Ort et al. 2008). Thirty-year annual mean precipitation and air temperature were 432 mm and 8.6°C, respectively (Classen et al. 2007). The dominant overstory vegetation consists of pinyon and one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg.) in a 3:1 ratio with a few rare ponderosa pines (*P. ponderosa* Dougl. ex Laws.), totaling 25–40% canopy coverage (Trotter et al. 2002). Pinyons in the study area grow to over 270 yr old, the majority being between 40 and 130 yr old (Trotter et al. 2002).

Study trees

We randomly selected 30 pairs of live moth-resistant and moth-susceptible trees. Paired trees were of similar age, and nearly all were <10–20 m apart (Fig. 2). This paired design maximized substrate and topography similarity to enable the most direct possible comparisons of the communities beneath moth-susceptible and resistant trees. Tree ring counts and growth rates indicate that

susceptible trees grow more slowly than resistant trees (Whitham and Mopper 1985). Thus, tree ages were assumed to be similar if susceptible trees were 20–30% smaller in trunk diameter than resistant trees. Trees lacking exposed rock substrate beneath their crowns were not considered, since rocks were essential lichen and bryophyte substrate in this study. Since this study focused on communities beneath tree crowns, we use the adjective “under-crown” to refer to the habitat beneath pinyons.

Community surveys

Lichen and bryophyte community data were recorded in three quadrats randomly placed beneath each of the 60 trees, for a total of 180 quadrats. For lichens and bryophytes, the average area surveyed under resistant and susceptible tree crowns was 3% and 4%, respectively. Quadrats were 0.25 m² and divided into nine cells. Relative cover of each saxicolous taxon was estimated to the nearest percent within each cell (Fig. 1) and then averaged across all cells to yield a cover for the quadrat. Lichen and bryophyte nomenclature followed Esslinger (2019) and Flora of North America (Flora of North America Editorial Committee 1993+), respectively. Voucher specimens were deposited into Northern Arizona University Herbarium (ASC).

Vascular plant communities were recorded in two 1-m² quadrats placed 1 m from the trunk on the north and south side beneath the crown of each of the 60 trees, for a total of 120 quadrats (Fig. 1). For vascular plants, the average area surveyed under resistant and susceptible tree crowns was 7% and 10%, respectively. Relative cover of each taxon was estimated to the nearest 1%. Vascular plant nomenclature followed Flora of North America (Flora of North America Editorial Committee 1993+) when treatments were available and Arizona Flora (Kearney and Peebles 1960) otherwise; updates from recent primary literature were applied.

Tree and environmental variables

Trunk diameter was measured about 50 cm above ground, and tree height and crown width were recorded to the nearest dm (Table 1). We measured photosynthetically active radiation (PAR) around noon on a cloudless day in May 2009 using a Sunfleck Ceptometer (Decagon, Pullman, Washington, USA). For each tree, five PAR measurements were made beneath each of the north and south sides of the crown, and an additional five were made in the open, for a total of 15 measurements. The mean of the under-crown measurements was divided by the mean of the open measurements, to yield a percent light availability beneath each tree's crown (Table 1). To characterize microhabitat within each 0.25-m² quadrat, we recorded relative cover of pinyon branches touching the ground, leaf litter, rocks <3 cm, and rocks >3 cm diameter (Table 1). Rocks <3 cm were

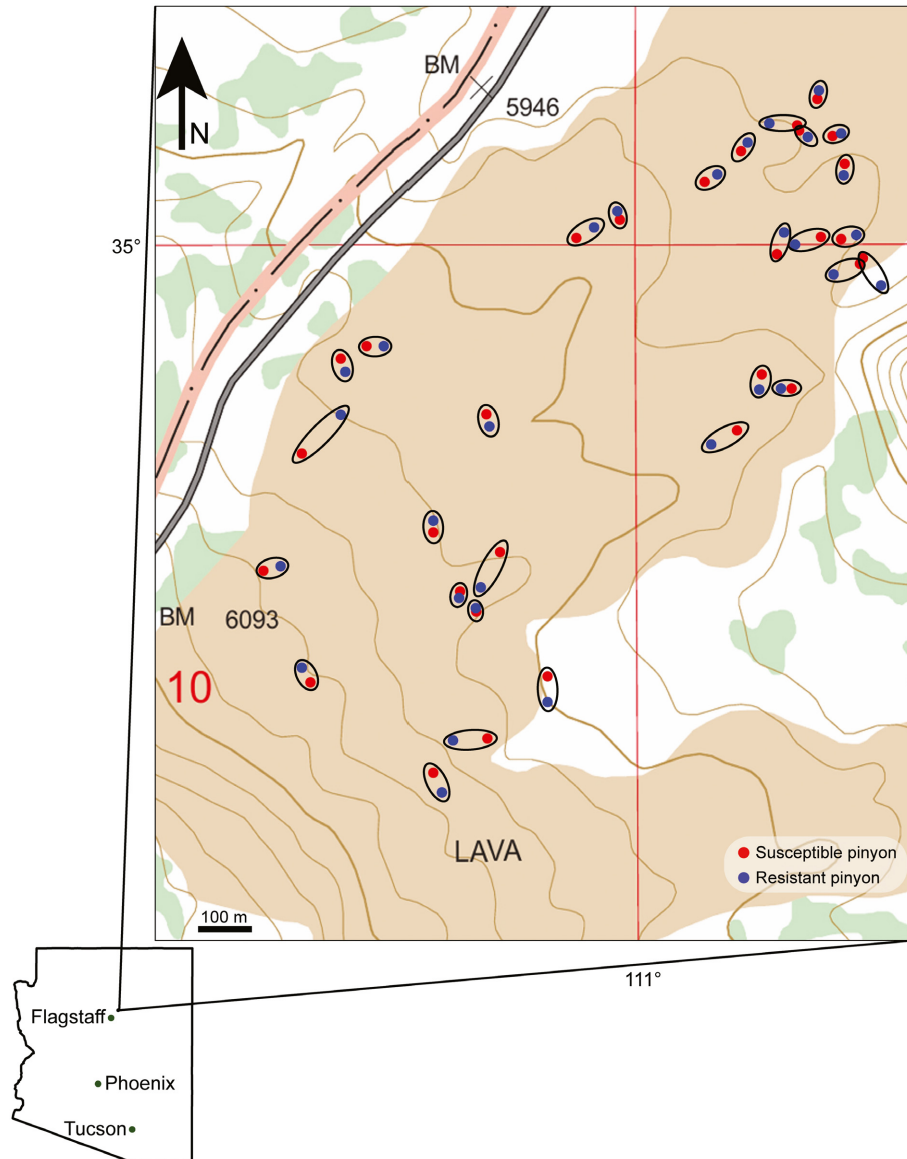


FIG. 2. Distribution of trees used in the study at Sunset Crater, Arizona, USA. Ovals associate pairs of moth-resistant and moth-susceptible trees. Contour line interval is 20 feet (1 foot = 0.30 m). Map generated using CalTopo with a USGS 7.5-minute quadrangle base map (www.CalTopo.com) and R (R Core Team 2021).

deemed too unstable to support slow growing saxicolous lichens and bryophytes.

Statistical analyses

Sampling completeness of the saxicolous and vascular plant communities was assessed using species accumulation curves. We used a sample-based rarefaction method to estimate the accumulation of species via successive addition of independent observational units (i.e., trees) (Colwell et al. 2012). These accumulation estimates were then used to generate species accumulation curves with confidence intervals for comparison of the accumulation

of species for all trees together and for resistant and susceptible trees separately. As all observations were conducted by pairing 30 resistant with 30 susceptible trees in close proximity, we conducted pairwise difference analyses. For univariate analyses of differences in tree traits (height, trunk, crown diameter) and under-crown environmental variables (litter, rock cover, branch cover, light availability), we conducted non-directional paired *t* tests (David and Gunnink 1997). Saxicolous and vascular plant community responses to moth susceptibility were examined by analyzing univariate and multivariate community metrics. Univariate metrics (percent cover, richness, Shannon's diversity index) were analyzed using

TABLE 1. Comparison of moth-resistant and moth-susceptible *Pinus edulis* trees at Sunset Crater, Arizona, USA.

Parameter	Resistant trees	Susceptible trees	<i>P</i>
Trunk diameter (cm)	43.1 ± 1.7	36.8 ± 1.0	0.0012
Height (cm)	388.3 ± 18.3	197.3 ± 6.4	<0.0001
Crown width (cm)	695.7 ± 34.7	548.7 ± 17.5	0.0001
Litter (%)	72.3 ± 4.4	87.3 ± 2.1	0.0077
Rocks >3 cm ² (%)	19.7 ± 3.2	10.1 ± 1.8	0.0200
Rocks <3 cm ² (%)	7.3 ± 2.2	2.3 ± 1.1	0.0465
Branches (%)	0.0 ± 0.0	0.1 ± 0.1	0.3256
Light (%)	25.3 ± 1.6	10.2 ± 0.9	<0.0001
Saxicolous cover (%)	2.75 ± 0.6	1.21 ± 0.4	0.0323
Saxicolous richness	6.03 ± 0.7	3.50 ± 0.5	0.0062
Saxicolous Shannon diversity	1.14 ± 0.1	0.70 ± 0.1	0.0207
Vascular plant cover (%)	24.88 ± 2.3	3.15 ± 0.6	<0.0001
Vascular plant richness	1.97 ± 0.1	0.40 ± 0.1	<0.0001
Vascular plant Shannon diversity	0.42 ± 0.1	0.03 ± 0	0.0002

Notes: Values are means ± SE. *P* values are the result of two-tailed, paired *t* tests. Significant *P* values are shown in bold-face font. Trunk diameter was measured 50 cm above ground. Litter, rock size, and branches refer to relative percent cover. Light represents the percent of photosynthetically active radiation (measured as number of photons·m⁻²·s⁻¹) under the tree crowns relative to unobstructed sky.

non-directional paired *t* tests (Pearson 1895) of the differences between resistant and susceptible trees. We also tested for the effect of moth susceptibility on each species to determine whether any species occurred more abundantly under either resistant or susceptible trees using non-directional paired *t* tests with *P* values adjusted with a false discovery rate procedure that accounted for repeated tests (Benjamini and Hochberg 1995). Multivariate community responses were analyzed with paired PERMANOVAs (Anderson 2001) using Bray-Curtis dissimilarity (Bray and Curtis 1957) adjusted to include zero-sum observations and 100,000 permutations. Mantel tests (Mantel 1967) were conducted to identify multivariate correlations between saxicolous and vascular plant community responses to moth susceptibility. Applying an ecological causal modeling approach (Grace and Bollen 2008), we constructed a priori models based on our hypotheses of the effects of tree traits on the saxicolous and vascular plant communities (Appendix S1: Fig. S1). To obtain community differences between tree pairs, the percent cover for each species from the resistant tree was subtracted from the value from the susceptible tree of the pair. These differences were used in the structural equation model (SEM) using linear regressions. Community response in the SEM was represented via nonmetric multidimensional scaling (NMDS) (Kruskal 1964) to generate ordinations of the community differences between tree pairs, using 100 random initial configurations with a

maximum of 1,000 iterations and a change in stress threshold of less than 10⁻¹². This was repeated for one- to four-dimensional configurations, and the configuration with the lowest dimensionality and an unexplained variation of less than 10% was selected. Ordinated scores were Procrustes rotated (Oksanen et al. 2019) for maximum correlation with the tree trait variables (Appendix S1: Fig. S2). Axis scores were then used in the structural model as community response variables. Models were fit to the standardized variables using a maximum likelihood estimator and a χ^2 goodness of fit test. We modeled saxicolous and vascular plant communities separately because we found no significant correlation between the response of the different communities to moth herbivory.

All analyses were performed with R version 4.0.4. (R Core Team 2021). Univariate *t* tests were conducted using the *stats* package (R Core Team 2021). Multivariate matrices were calculated using the *ecodist* package (Goslee and Urban 2007). PERMANOVA, Mantel tests, and the ordination with Procrustes rotations were executed using the *vegan* package (Oksanen et al. 2019). Structural equation modeling (SEM) was performed using the *lavaan* (Rosseel 2012) and *tidygraph* (Pedersen 2020) packages. Data and software for all analyses are deposited as a reproducible workflow using the *drake* package (Landau 2018) at Zenodo ([available online](https://doi.org/10.5281/zenodo.4531170)).⁸

RESULTS

Effects of moths on tree traits

Moth susceptibility affected tree traits, under-crown environments, and the saxicolous and vascular plant communities. Moth-resistant trees had significantly larger mean trunk diameter, height, and crown width (Table 1), consistent with other studies of this system (Whitham and Mopper 1985). Compared to resistant trees, leaf litter cover was 21% higher whereas light availability and exposed rock cover were 60% and 68% lower beneath susceptible trees (Fig. 3). Cover of pinyon branches touching the ground in the quadrats was unaffected by moth susceptibility. Neither litter cover nor exposed rock cover was correlated with light availability (Appendix S1: Fig. S3).

Lichen, bryophyte, and vascular plant responses

We registered 15 lichen, three bryophyte, and nine vascular plant species during the surveys (Appendix S1: Table S1). Three lichen species did not display reproductive structures and occurred in such small quantities that identification was deemed unreasonable. One vascular plant species remained unidentified. Species accumulation curves (Appendix S1: Fig. S4) indicated that the sampling of saxicolous and vascular plant communities

⁸ <https://doi.org/10.5281/zenodo.4531170>

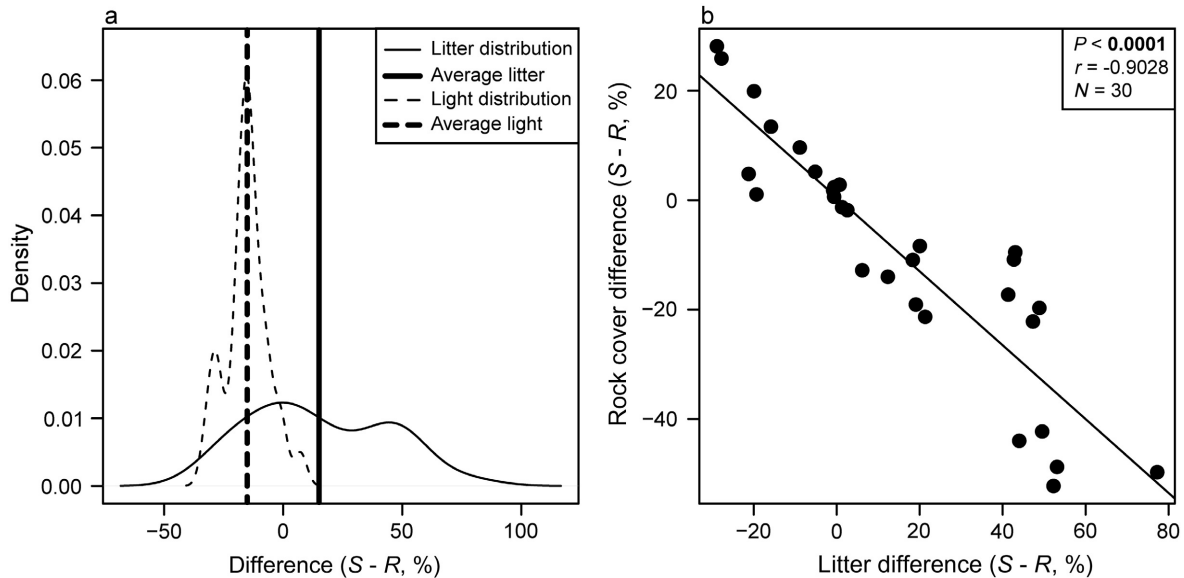


FIG. 3. (a) Density distribution of paired differences in leaf litter cover and light availability between moth-resistant (R) and moth-susceptible (S) trees shows that percent litter cover was greater under susceptible trees and light availability was greater under resistant trees. (b) Negative correlation between percent cover of exposed rocks (>3 cm) and percent cover of leaf litter.

under susceptible trees and saxicolous communities under resistant trees approached asymptotes, but had not yet plateaued, whereas the vascular plant curve from resistant trees was further from an asymptote. Saxicolous and vascular plant communities accumulated species slower beneath susceptible than resistant trees.

Saxicolous and vascular plant communities differed between resistant and susceptible trees with susceptible trees having 56% and 87% less cover, 42% and 80% less richness, and 38% and 92% less diversity, respectively, than resistant trees (Fig. 4, Table 1). Likewise, community composition of both saxicoles ($R^2 = 0.04$, $P = 0.0282$) and vascular plants ($R^2 = 0.31$, $P < 0.0001$) was predicted by moth susceptibility (Appendix S1: Table S2). Although the effect of moth susceptibility was significant for both saxicoles and vascular plants, their multivariate differences were not correlated (Mantel $r = -0.12$, $P = 0.44$). Three lichen species (*Acarospora americana* H. Magn. [$P = 0.0159$], *A. contigua* H. Magn. [$P = 0.0159$], and *Candelariella rosulans* (Müll. Arg.) Zahlbr. [$P = 0.0159$]) as well as two vascular plant species (*Brickellia californica* (Torr. and A. Gray) A. Gray [$P = 0.0020$] and *Fallugia paradoxa* (D. Don) Endl. ex Torr. [$P = 0.0007$]) covered significantly smaller areas beneath susceptible trees (Fig. 4; Appendix S1: Table S1).

Moth susceptibility indirectly influenced the saxicolous communities by impacting local environmental conditions via the cascading effects of moth herbivory on tree traits. The SEM fit the saxicole ($df = 13$, $\chi^2 = 18.54$, $P = 0.1380$) data well, as the model did not show significant differences between the implied and the observed covariance matrices. Moth susceptibility influenced the amount of litter, which in turn explained

significant proportions of the observed differences in the saxicolous communities as indicated by the total model variance (direct + indirect) explained by litter for each variable (percent cover $R^2 = 0.28$, richness $R^2 = 0.60$, diversity $R^2 = 0.54$). Crown size differences between resistant and susceptible trees also significantly influenced the saxicolous communities ($R^2 = 0.22$). The saxicole SEM supported a causal pathway from herbivory-induced increased litter cover that altered the availability of large rocks, ultimately affecting saxicolous communities (Fig. 5). Pathways involving light differences between resistant and susceptible trees were not supported in the saxicole SEM (Appendix S1: Table S3). Unlike the saxicolous communities, moth susceptibility did not appear to indirectly influence the vascular plant community via the measured variables. The vascular plant SEM indicated that neither light nor litter significantly affected any of the vascular plant community metrics (Fig. 5). Similar to the saxicolous model, the vascular plant SEM provided good model fit ($df = 7$, $\chi^2 = 9.76$, $P = 0.2026$), even though only the effect of tree crown on litter was significant (Fig. 5).

DISCUSSION

Our results demonstrate that the cascading effects of genetic variation in a foundation species can result in complex interactions among species (interspecific indirect genetic effects, IIGEs) that can alter community structure in unexpected ways. In support of our primary hypothesis, and as an example of how IIGEs influence trophic-independent, autotrophic organisms, we show that community composition of lichens, bryophytes, and

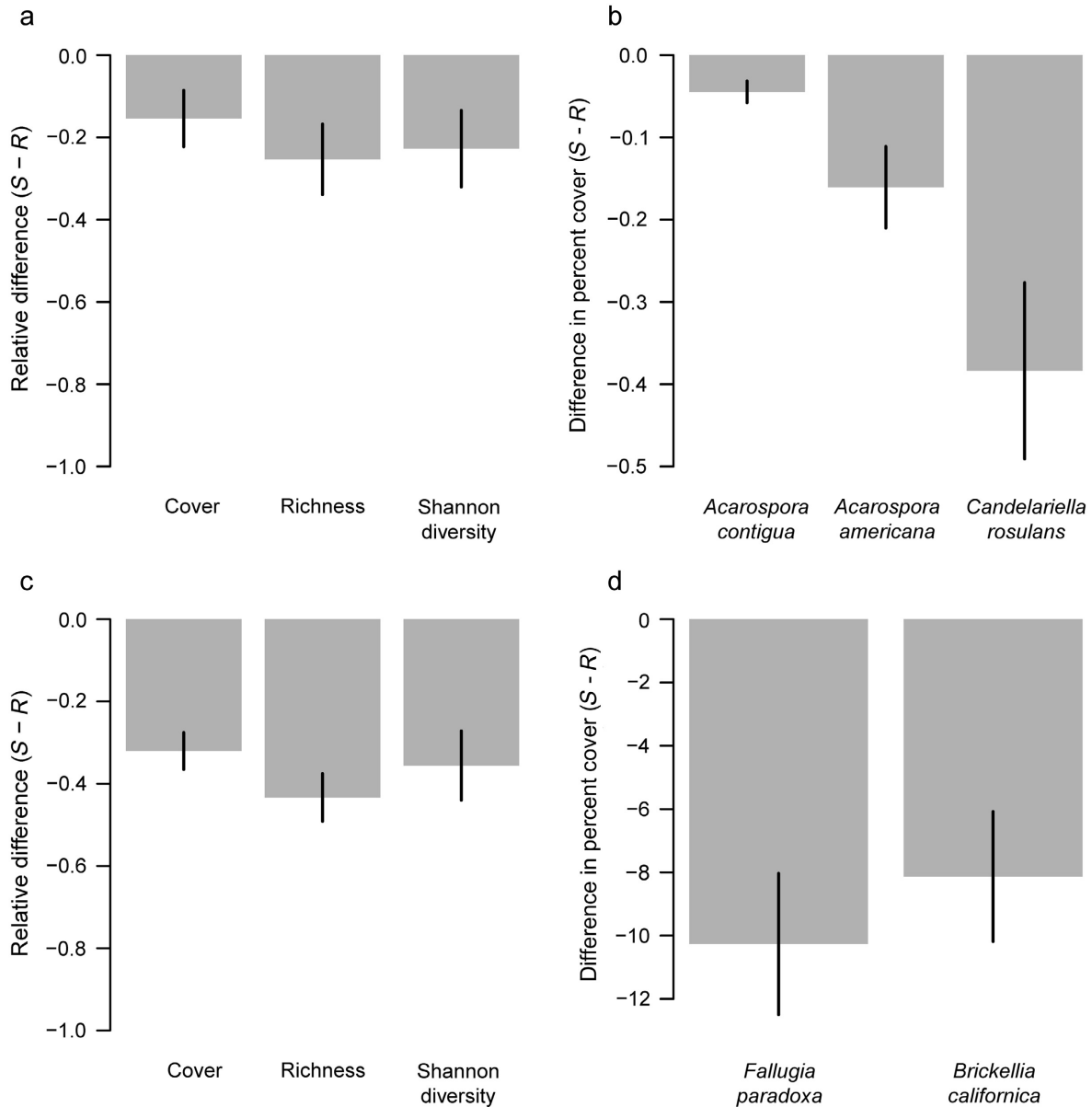
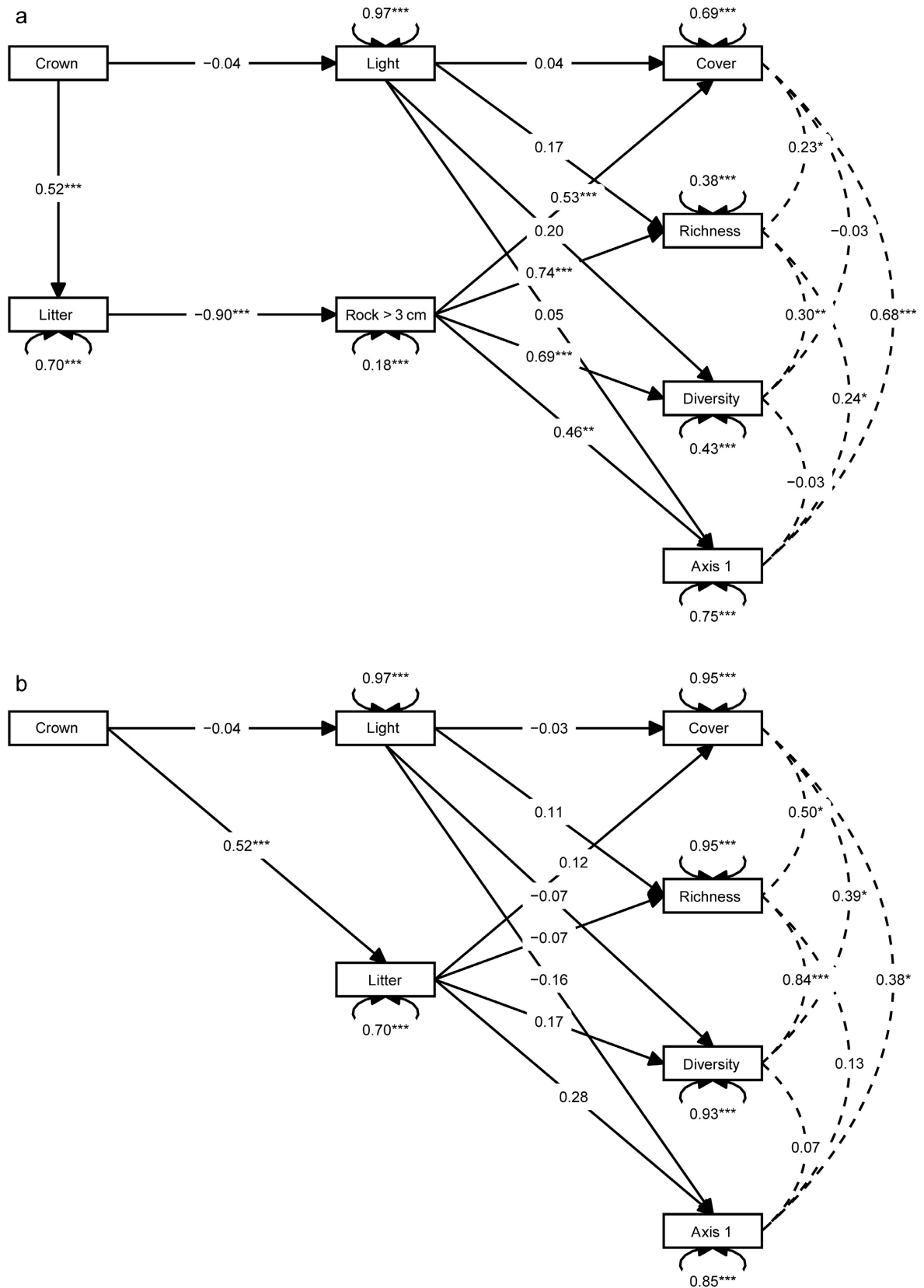


FIG. 4. Moth-susceptible trees (*S*) had significantly lower mean (a) saxicolous and (c) vascular plant percent cover, species richness, and diversity (Shannon’s index) than moth-resistant trees (*R*). Percent cover, richness, and diversity are relativized by dividing by the maximum absolute difference ($S - R$). (b) Average percent cover of three lichen species (*Acarospora contigua*, *A. americana*, and *Candelariella rosulans*) were significantly lower beneath susceptible trees, and (d) average percent cover of two vascular plant species (*Fallugia paradoxa* and *Brickellia californica*) were significantly lower beneath susceptible trees. Error bars are \pm SE.

vascular plants differed beneath the crowns of pinyons whose architecture is controlled by a genetically based interaction with stem-boring moths. Therefore, in this

arid system, genetic variation in a foundation conifer species results in IIGEs that, at a minimum, extend beyond the typical trophic cascade to include other

FIG. 5. Path diagrams of the structural equation models (SEM) for the (a) saxicolous and (b) vascular plant communities. Boxes are measured variables, each of which represents a paired difference between moth resistant and susceptible trees. Single-headed arrows show directional hypothesized causal links between variables with the standardized path coefficients overlaid onto their respective arrows. Asterisks indicate levels of significance based on maximum likelihood tests of individual pathways via linear regression (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Double-headed arrows and undirected dashed lines show the variances and covariances, respectively.



autotrophic organisms (i.e., the saxicolous and vascular plant communities). We propose that unravelling the interspecific indirect effects that originate from genetic variation in a foundation species is fundamental to understanding the ecology and evolution of complex ecosystems.

Interspecific indirect genetic effects

Interactions are central to our understanding of trophic structure, food webs, community organization, succession, and other basic ecological concepts. Interactions that are genetically based can affect the evolution of their respective communities and ecosystems. Communities associated with individual foundation species have the potential to evolve in response to changes in the local environment, a process known as “community evolution” (Whitham et al. 2020). For example, at Sunset Crater resistant and susceptible trees are dominated by different ectomycorrhizal fungal (EMF) communities, and importantly, these community differences are heritable because seedlings acquire the EMF communities of their parental group (Gehring et al. 2014, 2017). One realized consequence of this differential heritability is that climate selection favoring susceptible trees (Stultz et al. 2009b) has shifted the frequencies of both tree genotypes and their associated mycorrhizal mutualists that have positive feedbacks under drought conditions, producing a change of community phenotypes over time (Whitham et al. 2020).

In combination, the observed community differences of EMF, saxicoles, and vascular plants show genetically based IIGEs among trophic-dependent and independent communities that are rarely examined. The fact that otherwise trophic-independent organisms can have IIGEs, as our data indicate, suggests that such interactions may be quite common. Such genetic linkages of otherwise trophic-independent organisms argue that selection acting on the genetic variation in one organism can cascade via complex IIGE pathways to communities that otherwise would not be expected to interact. These findings also challenge key conceptual issues raised by Hubbell (2001, 2005) that communities can be viewed as assemblages of functionally equivalent and interchangeable units, and by Ricklefs (2008) that local communities have little to contribute to our understanding of ecology and evolution. Our findings would seem impossible if these hypotheses were correct.

Trophic-independent interactions

Understanding how intraspecific variation in a foundation species results in cascading effects on other communities has important implications for our perception of ecosystem connections (Whitham et al. 2020). Genetic variation tends to enhance diversity and productivity, stabilize ecosystem functions, and stimulate positive plant–soil interactions (Genung et al. 2010, Keith et al.

2010, Crutsinger 2016). Genetic variation in a foundation species has been shown to influence the ecology, dynamics, and evolution of associated dependent species and communities (Evans et al. 2008, Gehring et al. 2017, Whitham et al. 2020), and even extend to impact understory communities of vascular plants, autotrophic soil microorganisms, and epiphytic lichens (Adams et al. 2011, Lamit et al. 2011a, b, 2015b, Al Hayek et al. 2015, Selmants et al. 2019). These studies suggest that genetic variation in a foundation species can modify associated habitats and thus alter the composition of communities that do not rely on the foundation species for energy.

Genetic variation in pinyons causes some trees to be susceptible to herbivory and thus develop dense, flat-topped crowns because chronic attacks by stem-boring moth larvae selectively destroy terminal shoots, turning upright trees into shrubs (Whitham and Mopper 1985, Mopper et al. 1991, Brown et al. 2001). Our results indicate that large differences in crown size between resistant and susceptible trees leads to larger differences in litter abundance. The smaller, denser crowns of susceptible trees produce 21% more litter cover on average than the larger, thinner crowns of resistant trees (Fig. 1). The average leaf litter retention time at Sunset Crater is between 14 and 20 yr (Chapman et al. 2006; S. Chapman and A. Classen, *personal communication*); this long retention time in combination with extensive shading of the dense crowns, which decreases leaf litter degradation via ultraviolet light, may explain the higher leaf litter cover we found beneath susceptible trees. While moth carcasses and frass are potential nutrient inputs (Grace 1986), their influence under susceptible trees appears negligible. Instead, our data suggest that the extensive leaf litter cover on rocks beneath the tree crowns results in a combination of active smothering of the existing trophic-independent saxicolous communities and passive reduction of the amount of uninhabited exposed rocks. Available substrate for potential colonization is therefore decreased. This may be the primary cause of differences in community composition of saxicolous lichens and bryophytes beneath resistant vs. susceptible pinyons. Thus, our first subordinate hypothesis (increased litter accumulation beneath susceptible trees reduces cover, richness, and diversity of the saxicolous communities) was supported. Three lichen species in particular, *Acarospora americana*, *A. contigua*, and *Candelariella rosulans*, appear to be vulnerable to the conditions beneath susceptible trees, and the resulting decreased cover of these species was the main driver of the observed differences in saxicolous community composition between resistant and susceptible trees.

Similar to the effects observed for saxicoles, the vascular plant community was negatively affected by the under-crown habitat provided by susceptible trees as indicated by significantly lower cover, richness, and diversity under susceptible trees. However, our results failed to offer a causal pathway. While the saxicolous community depended on the presence of large rocks and

was negatively affected by higher litter cover, the vascular plant community was not affected by differences in litter or light between resistant and susceptible trees. The observed significant differences in vascular plant communities between resistant and susceptible trees may therefore have been caused by variables we did not measure, such as differences in under-crown mycorrhizal communities (Gehring et al. 2014, 2017) or concentration of allelopathic compounds known to suppress plant communities beneath pine trees (Kimura et al. 2015). Thus, neither our first nor our second subordinate hypotheses (increased litter accumulation and lower light availability beneath susceptible trees reduce cover, richness, and diversity of the vascular plant community) were supported. Nevertheless, two common vascular plants, *Fallugia paradoxa* and *Brickellia californica*, were significantly less abundant beneath susceptible trees, and they accounted for a large proportion of the observed difference in vascular plant community composition between resistant and susceptible trees.

Alternative pathways

While our data strongly suggest a pathway by which the impact of moth herbivory on genetically susceptible pinyons results in an under-crown environment that suppresses the saxicolous communities, we also considered alternative pathways that include the influences of light and microsite conditions. Surprisingly, after accounting for the effect of litter accumulation, the significant differences in light availability under resistant and susceptible trees did not influence the saxicolous lichen and bryophyte community composition. Thus, our second subordinate hypothesis (decreased available light beneath susceptible trees results in decreased saxicolous cover, richness, and diversity) was not supported. It is possible that the light environment at Sunset Crater may have been so bright that the under-crown differences had no influence on the distribution of species. However, average PAR under resistant and susceptible trees was 110 and 47 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively, and in arid habitats, lichens require PAR of about 70–120 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to gain positive net photosynthesis (Lange et al. 1998). Comparable data for bryophytes in arid habitats are unavailable, but most bryophytes reach 95% light saturation well below 1,000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Marschall and Proctor 2004). Instead, the lack of measurable light influence on the saxicolous community may be better explained by the fact that we measured light conditions under clear, sunny skies when these poikilohydric communities were dormant. That is, arid-adapted lichens and bryophytes very likely spend the bulk of their time photosynthesizing during precipitation events when clouds greatly increase diffuse light availability beneath forest canopies (Roderick et al. 2001). We therefore speculate that light conditions beneath resistant and susceptible trees may be more similar during rain events when the saxicolous communities are physiologically active.

Another alternative pathway we considered was that differences in microsite conditions, such as extremely nutrient-poor soils, could cause the shrub-like architecture exhibited by some trees. If true, the observed differences in saxicolous and vascular plant community composition could be the result of microsite variability rather than the cascading effects of genetic variation in pinyons. However, long-term moth exclusion from susceptible trees results in the same upright, monopodial architecture as resistant trees (Stultz et al. 2009a). Furthermore, our paired study design, in which we chose resistant and susceptible trees in close proximity, minimized the effect of microsite influence. We therefore find it highly unlikely that microsite variability was the driver of the observed differences in saxicolous and vascular plant community composition.

CONCLUSIONS

Our data show that the genotypic variability in pinyon that is responsible for resistance or susceptibility to herbivory by stem-boring moth larvae significantly affects the energy-independent saxicolous and vascular plant communities beneath their crowns. Therefore, heritable genetic variation in a foundation species can have widespread cascading effects via complex interspecific indirect genetic effects (IIGEs) that not only cross trophic levels but also extend to trophic-independent organisms. Although such complex genetic interactions are rarely examined, our findings provide a proof of concept for their examination in other ecosystems.

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SUPPORTING INFORMATION

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OPEN RESEARCH

Data and software for all analyses are deposited as a reproducible workflow using the *drake* package (Landau 2018) at Zenodo: <https://doi.org/10.5281/zenodo.5275318>